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# ON TWIN HYBRIDS

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In the group Onagra of the evening primroses the hybrids between different species are, as a rule, constant and uniform through the succeeding generations. In this respect they comply with the common rule for the majority of the characters of specific hybrids. Only, on account of the scarcity of regressive marks in this group, the phenomenon of constancy is allowed to show itself pure and complete. An exception is afforded by *Oenothera brevistylis*, the character of which splits up according to the formulae of MENDEL.[1]

As an example of a constant hybrid race I quote the *O. muricata*× *biennis*. It has been found uniform through at least four generations. In the second, the one in which Mendelian marks are seen to split, I cultivated over 80 flowering plants and over 100 rosettes, but no differences could be detected. Last summer (1907) I cultivated, on neighboring beds, 35 plants of the first and 18 of the fourth generation. Both groups produced a number of flowering stems, but, apart from the ordinary fluctuating variability, the characters were exactly the same in all the specimens. They had the flowers almost like those of *O. biennis*, but dense and richly flowered spikes like the *O. muricata*.

The types of the species used for this experiment were the forms which occur everywhere on waste places throughout Europe, having been introduced, the first from Virginia and the second from Canada, about three centuries and one century ago respectively. They are probably the types on which LINNAEUS based his descriptions of the species. In the United States, however, these Linnean species con-

[1] Die Mutationstheorie **2**:429.

sist of quite a number of subspecies, of which I collected over a dozen in Kansas, Missouri, Illinois, and elsewhere, during the summer of 1904. On sowing them in my experiment garden, I observed them to be fairly distinct, each constituting a sharply defined type. The form which is the most common throughout the United States is not the same as the one introduced into Europe, neither for *O. biennis* nor for *O. muricata*, as has also been pointed out by MACDOUGAL for *O. biennis*.

All these numerous elementary species agree with one another in a most interesting character. Their anthers touch the stigma, open themselves in the bud, and produce fertilization before the flower opens. The process is almost entirely finished before the insects are admitted. Crosses seem to be very rare in nature, although they do occur, since I collected the hybrid of *O. muricata* and *O. biennis* in the dunes near Amsterdam, and even more than once. A simple means of pure self-fertilization may be derived from this pollination within the bud. I cut the buds of our *O. biennis* one or two hours before opening, cutting through the middle of the tube, and the pods developed as strongly and produced as many good seeds as those whose flowers were allowed to be visited by bees. The flowers of *O. Lamarckiana*, *O. Hookeri*, and other large-flowered species, on the contrary, are not fertilized in the buds, but are in need of the help of insects (moths, bees, and bumble-bees).

The specific hybrids of this group of Onagra differ in a very conspicuous way from ordinary hybrids in so far as the reciprocal forms often are not identical, but differ widely from one another.[2] Although I have observed this fact in numerous cases, it is not a general rule. The hybrid *O. Lamarckiana*×*gigas* is identical with *O. gigas*×*Lamarckiana*. In the same way the species of the subgenus Euoenothera crossed with those of Onagra yield uniform hybrids. I crossed the *O. Sellowii* with *O. biennis*, *O. muricata*, and *O. Lamarckiana* and observed their reciprocal hybrids to be identical.

Within the group of the Onagras, however, the reciprocal hybrids are in most cases different, and with a few exceptions are more similar to their father than to their mother. They are, as it is called, patroclinous. So it is, for instance, with the reciprocal hybrids of *O. muri-*

[2] Die Mutationstheorie 2:471.

*cata* and *O. biennis* in their subspecies from our European dunes. The *O. muricata*×*biennis* looks like *O. biennis* and might be mistaken for it, since it is broad-leaved and large-flowered. The *O. biennis*× *muricata*, on the other hand, is narrow-leaved and small-flowered like its male parent. During the summer of 1907 I cultivated the first and second generations of the latter type and found them uniform, but in almost all respects different from the *O. muricata*×*biennis*. Especially the flowers are of a deep yellow and strongly scented, while those of *O. muricata*×*biennis* are pale and faintly scented.

This difference between the reciprocal hybrids is also clearly manifest in the crosses of *O. Lamarckiana* with the types of our dunes. The *O. Lamarckiana*×*biennis* has been described in my *Mutationstheorie* (**2**:31) for two generations, the third having only been cultivated in 1907. The *O. Lamarckiana*×*muricata* has been described and figured in the same volume (see page 29), but I have not as yet succeeded in getting a second generation, partly on account of the weakness of the type and partly on account of the general phenomenon of strongly diminished fertility in all these primrose hybrids.

The reciprocals of the two hybrids just mentioned afford the curious and rare phenomenon which I call that of the *twin hybrids*. In crossing one spike of *O. biennis* with the pollen of one plant of *O. Lamarckiana*, one does not get one but two hybrid types. The same holds good for *O. muricata*. These forms are intermediates between the parents and almost alike when seen from a distance, but sharply distinguished when closely examined. These differences are the same whether *O. biennis* or *O. muricata* is the mother plant, the hybrids showing their divergent origin only in apparently subordinate marks. One of the twins has broad and flat leaves of a bright green; I call it *O. laeta*. The other has narrow, more or less furrow-shaped leaves of a grayish green, which are more hairy, and is therefore designated *O. velutina*. These same names may be used to distinguish the twins in all the hybrid combinations in which they may occur.

The twin hybrids, *O. laeta* and *O. velutina*, occur in numerous hybrid combinations where *O. Lamarckiana* or one of its mutants is the pollen parent; as for instance with *O. brevistylis*, *O. rubrinervis*, and *O. nanella*. In these cases they drop, at least in the first

generation, the special mark of the mutant-father, and so are the same in all the cases named. The mother plant may be *O. biennis*, *O. biennis cruciata* (a form of *O. biennis* with linear petals which occurs in the dunes of Holland), *O. muricata*, or some other species of Onagra, although not all of them are capable of producing twins.

In the cases named the twins are widely different from their reciprocal hybrids, but closely related between themselves. Their characters often show transgressive fluctuability, and as a result of this they are more easily distinguished at some periods of their life than at others. The better the culture and the stouter the plants, the larger and more striking are the differences. Especially specimens which contrive to make a large rosette of root leaves before they send up their stem, and therefore begin flowering only late in the fall, are liable to display their differential marks in a most striking manner.

The twins are usually produced from the same cross in about equal numbers. On account of their highly diminished fertility it is difficult to get large cultures of their progeny, for even when the pods are large and contain an apparently full supply of seed, the germinating percentage is often very small. The following figures, however, will suffice to state the fact.

TABLE I

O. LAETA AND O. VELUTINA IN FIRST GENERATION

| Mother | Father | Number of progeny | Percentage of laeta | Percentage of velutina |
|---|---|---|---|---|
| O. biennis | ×O. brevistylis | 85 | 47 | 53 |
| O. biennis | ×O. rubrinervis | 50 | 42 | 58 |
| O. b. cruciata | ×O. brevistylis | 91 | 48 | 52 |
| O. muricata | ×O. Lamarckiana | 58 | 61 | 39 |
| O. muricata | ×O. brevistylis | 120 | 59 | 41 |
| O. muricata | ×O. nanella | 59 | 58 | 42 |
| | Average | | 52 | 48 |

In this experiment the parents have been those described above, and the crosses have been made by myself in the summer of 1905. The countings have been made during the flowering-season of 1907, only a small part of each of the cultures having remained rosettes; but the distinguishing marks in these were as evident in the fall, as those of the flowering plants. Some crosses, tried in previous years, had given the same results and prepared the method for an exact counting.

In the young plants, before the sending-up of the stems, it is of course easy to count far larger numbers of plants, but the influence of transgressive fluctuability is somewhat greater. I counted for *O. biennis*×*brevistylis* 287, for *O. biennis*×*Lamarckiana* 347, and for *O. biennis cruciata*×*brevistylis* 208 seedlings, and found 55 per cent., 60 per cent., and 64 per cent., or on an average 60 per cent. specimens of *O. velutina*, the remaining 40 per cent. being *O. laeta*. The figures, although from the cause given not as exact as those given above, evidently confirm the result.

Tried in the second generation, from artificially and purely self-pollinated seed, each of the twins yields a uniform progeny, with exactly the same characters as its parent. Therefore they may be considered as constant hybrid races. I made the majority of the crosses of the following table in 1903; had the first generation, which often consisted of only a few specimens on account of the diminished fertility, in 1905; and counted the forms in the second generation during the flowering-period of 1907. Most of the plants were counted in full flower, some of them, however, in the condition of rosettes of root leaves. Only for *O. muricata*×*brevistylis* the cross was made in 1905 and the second generation grown in 1906.

TABLE II

CONSTANCY OF O. LAETA AND O. VELUTINA IN SECOND GENERATION

| Cross | First generation | Second generation laeta | Second generation velutina |
|---|---|---|---|
| O. biennis×Lamarckiana | laeta | 13 | 0 |
| | velutina | 0 | 9 |
| O. biennis cruciata×Lamarckiana | laeta | 19 | 0 |
| | velutina | 0 | 3 |
| O. muricata×Lamarckiana | laeta | 4 | 0 |
| | velutina | 0 | 53 |
| O. biennis×rubrinervis | laeta | 30 | 0 |
| | velutina | 0 | 6 |
| O. biennis cruciata×rubrinervis | laeta | 22 | 0 |
| | velutina | 0 | 3 |
| O. muricata×brevistylis | laeta | 34 | 0 |
| | velutina | 0 | 57 |
| Total | | 122 | 131 |

I also tried this result by counting seedling plants as soon as they clearly showed their differentiating marks. From *O. laeta* seed I got

only *laeta;* from *O. velutina* seed only *velutina.* The observed cases for *O. laeta* were: *O. biennis*×*rubrinervis* (150), *O. biennis cruciata*× *Lamarckiana* (18), the same×*O. rubrinervis* (143); and for *O. velutina, O. muricata*×*Lamarckiana* (126), the same×*O. rubrinervis* (195), and the same×*O. brevistylis* (190). The figures in parentheses show the numbers of seedlings observed; together they give 311 seedlings of *O. laeta* and 511 of *O. velutina.*

It should be stated here that in the cross between *O. muricata* and *O. brevistylis* the character of the last-named species followed the Mendelian law in the case of both of the twins. The 34 *O. laeta* contained 30 per cent., and the 57 *O. velutina* 21 per cent., together also 26 per cent., of short-styled individuals, which bore in their leaves and flower-buds and in the flattened lobes of their stigma all the characteristics of their male grandparent. The *O. brevistylis* character is thereby shown to be independent of the hereditary units which cause the production of the twins.

The third and fourth generations have been cultivated in only one case, as yet, which was a cross made between *O. muricata* and the pollen of *O. Lamarckiana* in 1901. The *O. laeta* in this case was entirely sterile, and so only the *O. velutina* could be studied. It gave a constant progeny of small extent, the fertility in artificial self-pollination remaining in a diminished condition.

TABLE III

CONSTANCY OF O. VELUTINA DURING FOUR GENERATIONS

*Cross of O. muricata*×*O. Lamarckiana*

| Generation | O. laeta | O. velutina | O. laeta from O. velutina |
|---|---|---|---|
| Cross, 1901 | — | — | — |
| 1st generation, 1902 | 35 (sterile) | 35 | — |
| 2nd generation, 1903–4 | — | 27 | 0 |
| 3rd generation, 1905 | — | 53 | 0 |
| 4th generation, 1907 | — | 60 | 0 |

All in all 175 plants were observed, all bearing the same characters.

The phenomenon of twin hybrids seems to be very rare in plants. There can be do doubt that its occurrence in *Oenothera Lamarckiana* is intimately connected with at least part of the special manner in which this species displays its mutability. The production of some of the mutants seems to be quite dependent upon it, though that of

others is independent. But I must reserve an account of my experiments on this point for another occasion.

SUMMARY

1. Hybrids between members of the group Onagra or the *O. biennis* group of the evening primroses are, as a rule, constant in succeeding generations. An exception is *O. brevistylis*, the character of which follows MENDEL'S law.

2. The reciprocal hybrids of this group are, as a rule, unlike one another, and mostly patroclinous.

3. In many cases, where *O. Lamarckiana* or one of its derivatives is the father, two forms of hybrids are produced instead of one. These forms may be called twin hybrids.

4. One of the twins is broad and smooth-leaved and is called *O. laeta;* the other is more hairy and has furrow-shaped leaves, and is designated as *O. velutina.*

5. *O. laeta* and *O. velutina* are produced by the combinations *O. biennis*×*Lamarckiana* and *O. muricata*×*Lamarckiana,* and by those of some of their derivatives.

6. They are produced in about equal numbers.

7. They remain constant in the second generation. In the only ascertained case they also showed themselves so in the following generations.

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